

Cool-Season Grass Development Response to Accumulated Temperature under a Range of Temperature Regimes

P. W. Bartholomew* and R. D. Williams

ABSTRACT

Persistence and productivity of pastures containing mixtures of warm and cool-season forages may be compromised by interspecific competition when growing periods overlap. An ability to predict the onset and termination of growth of component species would facilitate timing of management interventions to minimize harmful competition in mixed pastures. Experiments were undertaken in controlled environment to assess the use of accumulated temperature values to indicate development stages in three cool-season grass species, and to evaluate the consistency of this relation under a range of temperature regimes that included variable exposure to below-freezing temperatures. When grown under light and dark temperature regimes of 22.5 and 7.5, 17.5 and 12.5, 15.0 and 0.0, or 10.0 and 5.0°C, respectively, leaf appearance in Italian ryegrass (*Lolium multiflorum* Lam.), tall fescue (*Festuca arundinacea* Schreb), and tall wheatgrass [*Elytrigia elongata* (Host) Nevskij] showed a close linear relationship with accumulated temperature, within each temperature regime. The interval between appearance of successive leaves on seedling mainstem (phyllochron) was increased by increased average daily temperature. In seedlings grown under a 15.0 and 0.0°C temperature regime, phyllochron was increased linearly by up to four 15-h exposures to -5.0 or -7.5°C dark-cycle temperatures in successive 24-h periods. The effects of variation in mean daily temperature and of plant exposure to below-freezing temperature on phyllochron should be considered if accumulated temperature is used to predict development stage of cool-season grasses in the field.

THE NEED TO REDUCE COSTS of livestock feeding has created interest in extending the grazing season and has resulted in increased use of cool-season forages in areas of the southern Great Plains (SGP) that have traditionally depended primarily on warm-season forage for livestock feed. However, in mixed pasture systems interspecific competition during transitions between warm and cool-season cropping may limit productivity or reduce persistence of some pasture components. Effective management of the transition from warm-season to cool-season production and vice versa depends, in part, on determining the developmental stage of component species in the pasture and when they begin and terminate growth. Although temperature threshold data are frequently used to determine the beginning and end of a growing season, average temperatures provide only an approximation of the actual dates at which crop growth starts and stops (Broad and Hough, 1993) and do not account for the effects on forage growth of day-to-day varia-

tion in temperatures. Accumulated temperature (growing degree days, GDD) is related to crop growth and development in cereals and grasses (Moore and Moser, 1995; Mitchell et al., 1997) and to the interval between appearance of successive leaves (phyllochron) in wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and forage grasses (Cao and Moss, 1989; Frank and Bauer, 1995; Kirby, 1995; Skinner and Nelson, 1995). Accumulated temperature values have been proposed as a means to predict harvest date and time of nitrogen application (Kowalenko et al., 1989) and for prediction of crop emergence in a warm- and cool- season grass mixture (Fidanza et al., 1996). Lemaire and Salette (1982) reported that spring vegetative growth of tall fescue and cocksfoot (*Dactylis glomerata* L.) was related to accumulated temperature and suggested that this relationship could be used to predict spring growth. Accumulated temperature values may be a more useful tool for prediction of onset or termination of growth than a single threshold temperature because they integrate day-to-day temperature variation through use of short-term historic (within cropping cycle) data. By convention, GDD accumulation for cool-season grasses and cereals is calculated as the accumulation above a mean daily temperature of 0°C and this may be justified by observations that leaf growth in many temperate forage species continues down to 0°C (Peacock, 1975a, 1975b, 1976; Parsons and Robson, 1980). However, at air temperatures associated with late fall and early spring, GDD accumulations above 0°C may be associated with a below-zero minimum temperature. The impact of diurnal temperature change on plant development and on response to accumulated temperature is not clear, particularly when plants are exposed to temperature minima that are at, or below, the limits to growth. The objectives of the work reported here were to determine whether the relation between accumulated temperature and leaf appearance in cool-season grasses remains constant over a range of temperature regimes characteristic of early and late growing season, and when plants are exposed to temperatures close to or below 0°C.

MATERIALS AND METHODS

Plant Materials and Growing Environment

Individual seedlings of Italian ryegrass cv. Marshall (IRG), tall fescue cv. Kentucky 31 (endophyte-infected) (TF), or tall wheatgrass cv. Jose (TWG) were used in all experiments. For all experiments, seedlings were grown in 155 mL "Containers" (Stuewe & Sons, Corvallis, OR) in Baccto potting soil (Michigan Peat Co., Houston TX), consisting of 900 g kg⁻¹ reed sedge peat + 100 g kg⁻¹ perlite and sand, as the growing medium. Plants were maintained in a growth chamber (Controlled Environments Inc., Pembina, ND) in a 13-h light

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and 11-h dark cycle and with an average photosynthetic photon flux density (PPFD) of $285 \mu\text{mol m}^{-2} \text{s}^{-1}$ at canopy height. Light input was monitored during each growing period with a quantum sensor (LI-COR Inc. Lincoln, NE). Seedlings were irrigated as necessary to keep the surface of the potting soil moist. At each irrigation, 10 mL of water was applied to each seedling. Growth chamber temperature regimes are specified below for each experiment and were imposed from planting so that for each experiment seed germination and seedling growth occurred under similar temperature conditions. In an initial set of experiments comparing the effect of temperature regime, daily maximum and minimum temperatures within the growth chamber were obtained from a mercury-in-glass maximum–minimum thermometer, read once each day. In all subsequent experiments growth chamber temperature data were recorded hourly to a HOBO datalogger (Onset Computer Corporation, Pocasset, MA) and an average value was calculated from temperatures recorded at four probes sited among the seedlings. The maximum (T_{max}) and minimum (T_{min}) average temperature values recorded in each midnight-to-midnight 24-h period were used to calculate accumulated temperatures during each experiment. Accumulated temperature was calculated as the accumulation of mean daily temperature after seedling emergence $(T_{\text{max}} + T_{\text{min}})/2$ above a base temperature (T_{base}) of 0°C ; thus accumulated temperature (Growing Degree Days, GDD) = $\sum[(T_{\text{max}} + T_{\text{min}})/2] - T_{\text{base}}$. Incubator air temperatures and soil temperatures in cones during cold treatment were recorded hourly to a datalogger with two temperature probes positioned adjacent to cones (for air temperature measures) and with two probes inserted vertically to 2-cm depth to estimate soil temperatures.

Temperature Regime and Species Effects on Leaf Appearance

Seedlings were grown under four temperature regimes consisting of light- and dark-cycle temperatures of 22.5 and 7.5, 17.5 and 12.5, 15.0 and 0.0, or 10.0 and 5.0°C . These regimes correspond to average daily temperatures of 7.5 and 15.0°C , at diurnal temperature ranges of 5 and 15°C . At each temperature regime the cumulative leaf appearance on the mainstem of each of five replicate seedlings was measured up to 350 GDD after emergence. The total number of leaves visible on each seedling mainstem was counted and recorded three to five times per week throughout each experiment. Leaf appearance response to accumulated temperature for each species in each temperature regime was calculated by linear regression of the mean cumulative number of visible leaves for each group of five seedlings using post-emergence accumulated temperature above a base of 0°C as the independent variable. The mean interval (phyllochron, GDD leaf^{-1}) between appearance of successive leaves for each treatment group was calculated as the reciprocal of the appropriate linear regression coefficient. Comparisons of treatment effects on phyllochron were made by analysis of variance, considering temperature regimes (partitioned into main effects of average and temperature range), species, and the temperature regime \times species interaction. Replication of treatments was provided by two repetitions in time of each set of four temperature regimes. Individual mean comparisons were made by LSD ($P \leq 0.05$), using the procedures of Genstat (2002).

Exposure to Below-Freezing Air Temperatures and Leaf Appearance in IRG

A sequence of experiments was conducted with seedlings of IRG to assess the temperature sensitivity and response of

leaf appearance to cold exposure. Individual seedlings of IRG were grown, as described above, within a temperature regime of 15.0 and 0.0°C light- and dark-phase temperatures. Replicate groups of five seedlings were maintained at the growth chamber temperature regime or, at 105 to 165 GDD post-emergence (between 2nd and 3rd leaf appearance) were exposed once or twice in successive 24 h periods to dark-cycle air temperatures of -2.5 , -5.0 , or -7.5°C . Each cold treatment was made by transferring seedlings to a low-temperature incubator for 15 h, throughout the dark phase of the growth chamber diurnal cycle. At each below-freezing temperature treatment Cone-tainers were either insulated against the cold or exposed in unprotected in Cone-tainer trays. Insulation was provided by a polystyrene seedling block that was modified to allow insertion of 155-mL Cone-tainers so that the soil column was surrounded by insulating material. At the end of each period of cold-exposure, treated seedlings were returned to the growth chamber to resume the 15.0 and 0.0°C temperature regime. All combinations of low temperature, cold protection, and frequency of exposure were examined, with the exception of two exposures to -7.5°C in unprotected Cone-tainers, for a total of 12 treatment comparisons. Mean mainstem leaf appearance rate of each treatment group of five seedlings was calculated as described above. All cold treatments were repeated two or three times in separate experiments, together with a no cold treatment control for which plants were maintained continuously under the $15/0^{\circ}\text{C}$ growth chamber temperature regime. Treatment effects on leaf appearance were analyzed as a completely randomized design and mean separation was estimated by LSD (Genstat, 2002).

Cumulative Effect of Exposure to Below-Freezing Temperatures on Leaf Appearance and Leaf Extension Rates in IRG, TF, and TWG

The effects of no cold treatment or of successive daily 15-h exposures to -5.0 or -7.5°C air temperatures for 1, 2, 3, or 4 d on leaf and tiller appearance and on leaf extension rates were measured in seedlings of IRG, TF and TWG grown in a 15.0 and 0.0°C light- and dark-phase temperature regime. Experimental procedures were the same as those used for IRG experiments described above, except that all seedlings were grown in Cone-tainers that were insulated during exposure to below-freezing temperatures. The leaf appearance on each seedling mainstem was recorded and the mean phyllochron for each group of five replicate seedlings was calculated as described above. Cumulative tiller appearance on each seedling was also determined each time that leaf appearance observations were made. The mean extension rate of the first two leaves that emerged on each mainstem following cold treatment was estimated from repeated measurements of leaf lamina length on the fourth and fifth leaves on IRG seedlings, and on the third and fourth leaves of TF and TWG seedlings. Measures on five replicate plants were used to calculate the mean rate of leaf extension (mm GDD^{-1}) over a period of 70 GDD following appearance of each measured leaf by regression of lamina length against accumulated temperature (GDD).

Cold treatment and species effects on phyllochron and leaf extension rates were analyzed as a factorial experiment of 30 treatments (five cold exposure levels \times three species \times two minimum temperatures) replicated twice in time. Statistical analysis used the mean values of phyllochron and leaf extension rate for each treatment group of five plants and mean separation was estimated by *F*-protected LSD. The effect of cold treatment on cumulative tiller number was evaluated by regression of $\ln(\text{tiller number})$ against accumulated tempera-

ture and by comparison of the fitted slopes for each frequency treatment within species (Genstat, 2002).

RESULTS

Temperature Regime and Species Effects on Leaf Appearance

In all species tested, the rate of leaf appearance displayed a highly significant ($P < 0.001$) linear relationship with post-emergence accumulated temperature above 0°C and for individual species of grass this linear relationship explained 88 to 97% of variation in mainstem leaf appearance. The response of IRG (mean $r^2 = 0.95$) was consistently less variable than that of TWG and of TF. The mean rate of leaf appearance in IRG was significantly higher than that of TF and TWG, and the phyllochron for each species was estimated at an average over all temperature regimes of 69, 89, and 95 GDD leaf $^{-1}$ for IRG, TF and TWG, respectively (LSD 8.3, $P = 0.05$). The species \times temperature regime interaction was not significant ($P > 0.05$) and only main effects of temperature regime are presented in Fig. 1. On average, over the three species the phyllochron increased with increased daily maximum temperature, irrespective of average daily temperature (Fig. 1).

The mean phyllochron was increased by a higher average daily temperature and by a greater daily temperature range (Fig. 2). Neither the species \times average temperature nor the species \times temperature range interaction was significant ($P > 0.05$).

Exposure to Below-Freezing Air Temperatures and Leaf Appearance in IRG

Observed cone and air temperatures are presented in Fig. 3 as the number of hours that measured tempera-

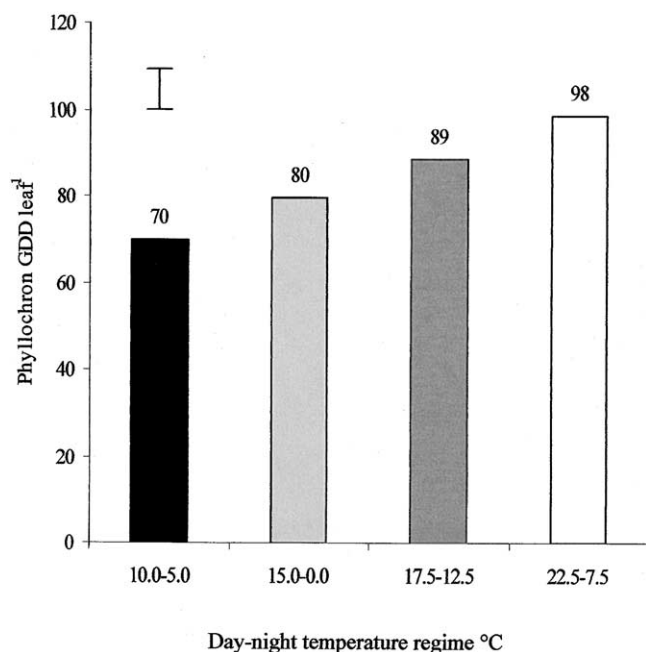


Fig. 1. Effect of temperature regime on mean phyllochron (GDD leaf $^{-1}$) in Italian ryegrass (IRG), tall fescue (TF), and tall wheatgrass (TWG). Vertical bar indicates LSD = 9.3 ($P = 0.05$) for comparisons of means.

tures in air uninsulated and insulated cones were below 0, -1.0 , and -2.0°C , within a 15-h exposure period. Over a 15-h period of cold treatment, the insulation of individual Cone-tainers in polystyrene reduced the time that soil temperatures were below -1.0 and -2.0°C , and therefore reduced cumulative cold-exposure of the below-surface plant parts.

Leaf appearance rate in IRG seedlings was not significantly reduced ($P > 0.05$) by a single or double exposure to -2.5°C for 15 h in uninsulated Cone-tainers, compared with the rate observed with nonexposed plants. When plants in uninsulated Cone-tainers were exposed to -5.0°C for 15 h, a single exposure was sufficient to reduce leaf appearance rate, compared with nonexposed plants ($P < 0.05$). A double exposure to -5.0°C cold treatment further reduced leaf appearance rate, although the effect was significant only at $P = 0.15$. A single cold treatment of -7.5°C for 15 h killed seedlings exposed in uninsulated Cone-tainers. In contrast, plants in Cone-tainers that were insulated during cold treatment showed no significant ($P > 0.05$) effect on leaf appearance rate of single or double exposure to temperatures as low as -7.5°C over a 15-h period, compared with plants that were not exposed to below-freezing temperatures (Fig. 4).

Cumulative Effect of Exposure to Below-Freezing Temperatures on Leaf Appearance and Leaf Extension Rates in IRG, TF, and TWG

At the start of cold treatment IRG, TF, and TWG seedlings showed averages of 3.4, 2.6, and 2.9 emerged leaves on each mainstem. All seedlings survived the 15-h exposure to air temperatures of -5.0 or -7.5°C up

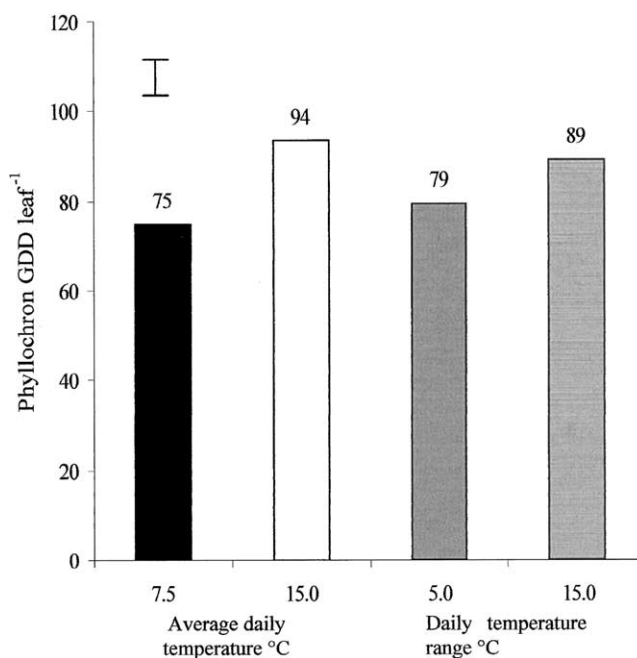


Fig. 2. Effect of average daily temperature and daily temperature range on mean phyllochron (GDD leaf $^{-1}$) in Italian ryegrass (IRG), tall fescue (TF), and tall wheatgrass (TWG). Vertical bar indicates LSD = 6.8 ($P = 0.05$) for comparison of means of average temperature or of daily temperature range treatments.

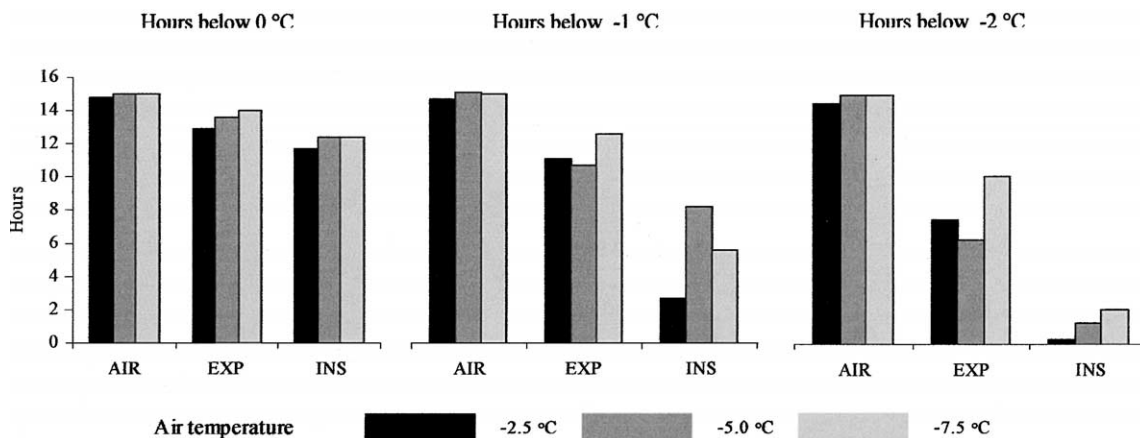


Fig. 3. Effect of air temperatures of -2.5 , -5.0 , or -7.5°C and of insulation of Cone-tainers on the duration of exposure to air and soil temperatures of 0 , -1 , or -2°C of Italian ryegrass seedlings: AIR = air temperature indicated by probes positioned adjacent to seedling leaves, EXP = soil temperature indicated by probes inserted into soil in an uninsulated Cone-tainer, INS = soil temperature indicated by probes inserted into soil in a Cone-tainer insulated in a block of polystyrene.

to four times in successive 24-h periods. As frequency of exposure to below-freezing temperature increased, the mean phyllochron increased by an average of 35% ($P < 0.001$) in up to four exposures. Average phyllochron of treatments exposed to -5.0°C was slightly lower (i.e., rate of leaf appearance was slightly higher) than on those exposed to -7.5°C , but the difference was not significant ($P > 0.05$). There was no significant difference among species ($P > 0.05$) in response to frequency of exposure or to level of exposure, therefore only main treatment effects are summarized in Table 1.

The effect of repeated exposure of seedlings to cold treatment on rate of increase in tiller number was qualitatively similar to the effect on leaf appearance, with tiller appearance rate reduced as frequency of exposure

increased (Table 2). Decrease in minimum temperature reduced rate of tiller appearance, but the difference between minima of -5.0 and -7.5°C was not significant ($P > 0.05$).

Exposure of up to four nights of -5.0 or -7.5°C air temperature reduced rates of leaf extension in each species by an average of 0.19 mm GDD^{-1} for each 15-h exposure to below-freezing temperature. Reducing minimum air temperature from -5.0 to -7.5°C also significantly ($P < 0.001$) decreased mean rate of leaf extension (Table 1).

DISCUSSION

The results are consistent with other research with small-grain cereals and forage grasses (Bahmani et al., 2000; Cao and Moss, 1989; Kirby, 1995) where leaf appearance follows a close linear relationship with accumulated temperature. The data presented are those of leaf appearance on mainstem only; therefore, phyllochron values may differ from those obtained from a tiller

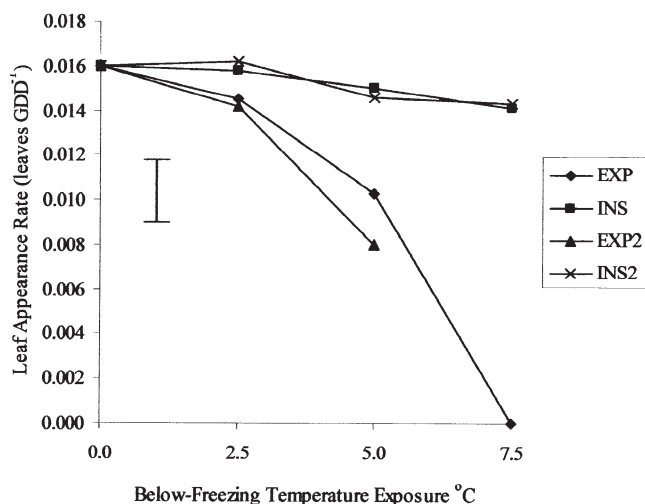


Fig. 4. Leaf appearance rate (leaves GDD^{-1}) in Italian ryegrass following single or double 15-h exposure to minimum temperatures of -2.5 and -5.0°C , a single exposure to -7.5°C or in a control treatment maintained at the growth chamber temperature regime with minimum night temperature of 0°C . EXP = single 15-h exposure in uninsulated Cone-tainer, EXP2 = two 15-h exposures in uninsulated Cone-tainer, INS = single 15-h exposure in insulated Cone-tainer, INS2 = two 15-h exposures in insulated Cone-tainers. Vertical bar shows $\text{LSD} = 0.0033$ ($P = 0.05$) for comparison of means.

Table 1. Effect of repeated exposure to air temperatures of -5.0 or -7.5°C on phyllochron (GDD leaf^{-1}) and on rate of leaf extension (mm GDD^{-1}) of Italian ryegrass (IRG), tall fescue (TF), and tall wheatgrass (TWG).

Main treatment effects	Phyllochron $\text{GDD leaf}^{-1}\dagger$	Rate of leaf extension $\text{mm GDD}^{-1}\dagger$
Number of 15-h exposures to air temperatures below freezing		
0	72.7a‡	1.53a‡
1	79.8ab	1.35b
2	84.2bc	1.19b
3	88.3cd	1.01c
4	98.2d	0.78d
Low temperature exposure		
-5.0°C	82.1a§	1.29a§
-7.5°C	87.2a	1.06b
Species		
IRG	75.1a#	1.37a#
TF	88.8b	0.79b
TWG	90.0b	1.36a

† Within treatment (number of exposures ‡, low temperature treatment §, species #) means followed by the same letter are not significantly different according to LSD at $P = 0.05$. Interactions between treatments were not significant ($P \leq 0.05$).

Table 2. Relationship of tiller appearance and accumulated temperature in Italian ryegrass (IRG), tall fescue (TF), and tall wheatgrass (TWG) with up to four 15-h exposures to air temperatures below freezing (means of exposures at -5.0 and -7.5°C).

IRG	0 exposure	$\ln(\text{tiller}) = 0.0085\text{GDD} - 0.80$
	1 exposure	$\ln(\text{tiller}) = 0.0085\text{GDD} - 0.83$
	2 exposures	$\ln(\text{tiller}) = 0.0072\text{GDD} - 0.58$
	3 exposures	$\ln(\text{tiller}) = 0.0072\text{GDD} - 0.63$
	4 exposures	$\ln(\text{tiller}) = 0.0068\text{GDD} - 0.61$
		SE(slope) 0.0004: R^2 87.7
TF	0 exposure	$\ln(\text{tiller}) = 0.0065\text{GDD} - 0.91$
	1 exposure	$\ln(\text{tiller}) = 0.0059\text{GDD} - 0.80$
	2 exposures	$\ln(\text{tiller}) = 0.0058\text{GDD} - 0.77$
	3 exposures	$\ln(\text{tiller}) = 0.0050\text{GDD} - 0.70$
	4 exposures	$\ln(\text{tiller}) = 0.0049\text{GDD} - 0.70$
		SE(slope) 0.0004: R^2 78.5
TWG	0 exposure	$\ln(\text{tiller}) = 0.0079\text{GDD} - 1.10$
	1 exposure	$\ln(\text{tiller}) = 0.0076\text{GDD} - 1.02$
	2 exposures	$\ln(\text{tiller}) = 0.0066\text{GDD} - 0.91$
	3 exposures	$\ln(\text{tiller}) = 0.0065\text{GDD} - 0.91$
	4 exposures	$\ln(\text{tiller}) = 0.0058\text{GDD} - 0.88$
		SE(slope) 0.0005: R^2 78.2

population with a more diverse age structure, as noted by Gan and Mcleod (1997), with rye (*Secale cereale* L.). However, the objective of the work reported here was to measure changes in phyllochron in response to a changing temperature environment, rather than to define a single phyllochron value for the species studied. Results from temperature regime studies demonstrated that, within a 0 to 22.5°C range of temperatures, leaf appearance rate did not maintain a constant relation with accumulated temperature and phyllochron was increased by an increase in mean daily temperature. This result is consistent with results reported for wheat and barley (Cao and Moss, 1989; Frank and Bauer, 1996) and with tall fescue (Durand et al., 1999). Phyllochron also appeared to increase with increased daytime (light-phase) temperature and, on the basis of this observation, an increase in phyllochron apparently resulting from an increase in diurnal temperature range from 5 to 15°C could be explained by differences in mean daily high temperature (13.75 and 18.75°C) associated with the temperature range treatments. However, light-phase temperature levels were confounded with dark-phase temperature treatments and changes observed in phyllochron cannot be attributed solely to change in mean daily high temperature without further verification.

Few experiments, other than those performed in the field at ambient temperatures, have examined the effects of varying light- and dark-phase temperatures on phyllochron. The phyllochron values observed here were comparable with other estimates for the forage species used. Frank and Bauer (1995) reported estimates of phyllochron ranging from 94 to 148 GDD leaf $^{-1}$ for wheatgrasses (*Elytrigia* spp) grown in the field and, at comparable GDD accumulation, the values observed in TWG in the experiments reported here fell within this range with an average 110 GDD leaf $^{-1}$. Estimates of phyllochron values for TF grown at constant temperatures in a controlled environment range from approximately 100 GDD leaf $^{-1}$ at 20°C (Skinner and Nelson, 1994) to 280 GDD leaf $^{-1}$ at 24°C (Durand et al., 1999). An estimate of 88.5 GDD leaf $^{-1}$ for the phyllochron of field-grown IRG (Ball et al., 1995) was higher than values observed

with IRG in our experiments, but was based on observations that included winter and may reflect the effect of repeated exposure to low temperatures as discussed below.

In temperature regime comparisons, seedlings were not exposed to temperatures below 0°C . However, in early spring and late fall in the southern Great Plains mean daily temperatures that appear adequate for plant growth may be associated with minimum temperatures below freezing. Results showed that growth and development of cool-season grasses could continue with a positive temperature accumulation above 0°C , in spite of exposure to below-freezing temperature. The experiments also demonstrated that the effect of below-freezing temperature on reduction in leaf appearance and leaf extension rates was cumulative and, in the case of leaf extension rate, temperature-dependent. Therefore any value of phyllochron applied to prediction of grass phenology would need correction for the frequency of exposure to below-freezing temperature. Measurement of mainstem leaf appearance shows only the short-term effects of low temperature treatment. However, a reduction in the rate of tiller appearance is an expected consequence of reduced leaf appearance and tiller site formation (Davies and Thomas, 1983). Together with a reduced rate of leaf extension (through an effect on assimilation) the reduction in tiller appearance rate suggests that the effect of below-freezing cold exposure will manifest itself in reduced rates of plant development beyond mainstem leaf appearance.

Comparison of responses to cold exposure in insulated and uninsulated cones shows that, at least to air temperatures as low as -7.5°C , below-surface cold exposure has a greater influence on leaf appearance than air temperature. This result is consistent with observations made by Peacock (1975b). Incubator cold treatment only partly simulated cold exposure in the field. Even with insulation of Cone-tainers, cold treatment of individual plants in the incubator provided a more extreme below-surface cold exposure than plants are likely to experience in the field in the Southern Great Plains. In Cone-tainers, although the duration of exposure to freezing temperature at a depth of 2 cm was reduced by insulation, minimum temperatures generally dropped as low as the surrounding air temperature within a 15-h exposure period. In contrast, field soil temperatures in central Oklahoma during the winters of 2001–2002 and 2002–2003 never fell below -2.0°C at 2 cm below the soil surface, even though air temperature minima as low as -15.4°C were recorded (Bartholomew, unpublished). Long-term (50-yr) meteorological records in central Oklahoma (Climatedata, 2002) show average annual minimum air temperatures of -17.4°C , with a range of -10.7 to -25.0°C , so plant exposure to cold in the field is likely to be characterized by more extreme aerial exposure and less extreme below-surface exposure than with plants grown in Cone-tainers under the temperature regimes we used. The impact of differences in cold exposure on phyllochron estimates in growth chambers and in the field requires further investigation.

CONCLUSIONS

These experiments were undertaken to assess whether accumulated temperature could be a useful indicator of forage grass development at temperatures close to the lower limits for growth and, therefore, as an indicator of the onset or termination of growth in the field.

The value of accumulated temperature as an indicator depends on how reliably it will predict plant phenology over varying average daily temperatures. Although the relation of accumulated temperature and mainstem leaf number was linear at all temperature regimes, differences in slope indicate that a single phyllochron value is not appropriate for estimation of development rate under a wide range of temperature regimes. Within a narrower range of temperatures typical of the early growing season in the southern Great Plains, phyllochron values were relatively consistent and may allow use of accumulated temperature as an indicator of onset of early season growth. However, exposure of cool-season grasses to below-freezing temperatures increases the phyllochron and this effect shows that days with accumulated temperature values below 0°C do not have a neutral effect on plant development, as implied by the attribution of a phyllochron value of zero for all mean daily temperatures below 0°C in conventional calculations of accumulated temperature. Additional work needs to be done to assess whether modification of the computation of accumulated temperature to make allowance for exposure to below-freezing temperatures would improve the predictive quality of accumulated temperature values.

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